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Habitat selection of the Mauritian lowland forest day gecko at multiple spatial scales: A baseline for translocation

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ABSTRACT

Of 30 known subpopulations of *Phelsuma guimbeaui*, 18 are in patches of exotic forest and are predicted to disappear in the next decade. One possible means of mitigating the reduction in genetic diversity associated with the loss of subpopulations is to translocate "at risk" subpopulations to more secure habitats. Prior to any such intervention, it is important to identify a species' basic ecological needs. We had three main objectives: to calculate home range sizes of adult geckos; characterise habitat selection among age groups; and identify the order of importance of each habitat predictor. Habitat selection of *P. guimbeaui* was explored at the population, home range and microhabitat levels. Males had larger home ranges than females, and overlapped temporally with more females than males. We showed that habitat selection differed between age groups. In order of importance, tree diversity, tree species, tree height, trunk dbh and cavity density were important habitat predictors. We discuss how these data can be used to inform the choice of sites for the translocation of threatened subpopulations. Our results also highlight the importance of undertaking habitat restoration for the long-term conservation of the 12 subpopulations that survive in patches of endemic forest.

1. Introduction

Habitat selection is "the process of choosing a habitat" (Johnson, 1980) and is key to understanding animal behaviour, population dynamics (Strickland and McDonald, 2006), animal-habitat associations essential for reproduction and survival (Manly et al., 2002), and ultimately for informing species management. Identifying the critical spatial needs of threatened species allows more efficient management and conservation plans to be developed. Habitat selection is usually explored at hierarchical spatial scales (De La Cruz et al., 2014; Hódar et al., 2000; Oppel et al., 2004) because selection can

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vary with scale (Johnson, 1980). Thomas and Taylor (1990) identified three spatial scales: the population level, where habitat selection is inferred at a landscape level or within the study area; the home range level, which involves the selection of a home range within an area; and the microhabitat level, which represents selection of a particular habitat resource within the home range. The combined use of different hierarchical scales helps identify important predictors of habitat use (Beasley et al., 2007) and is essential for species management (Razgour et al., 2011).

In Mauritius, endemic reptiles provide a range of key ecological services such as pollination and seed dispersal, and are important prey species (Cheke and Hume, 2008; Hansen and Müller, 2009). Only five of 17 endemic reptile species still persist on mainland Mauritius (Arnold, 2000; Austin et al., 2004; Rocha et al., 2009), and of these *Phelsuma guimbeaui* (lowland forest day gecko) is the most vulnerable to extinction (Buckland et al., 2014a,b). It isrestricted to 30 small and isolated subpopulations (Supplementary data Fig. A1 in Appendix A). Effective population size (i.e. the number of individuals that can potentially breed in a randomly mating population) ranged between 44 and 167 for ten of these subpopulations (Buckland et al., 2014b). Based on habitat area, the other 20 subpopulations are likely to have effective population sizes within this range. Habitat loss appears to have been the main cause of the decline and fragmentation of *P. guimbeaui* populations.

Several invasive predators and competitors also threaten subpopulations of *P. guimbeaui* and other endemic species of *Phelsuma* (Cheke and Hume, 2008; Cole and Harris, 2011). The recent introduction of *Phelsuma grandis* (giant Madagascar day gecko), an ecologically similar introduced gecko predator/competitor (Cole, 2009; Buckland et al., 2014a), and continuing habitat degradation and genetic erosion (Buckland et al., 2014b), are likely to cause further population declines. Of the 30 remaining subpopulations, 18 are in patches of exotic forest and at imminent risk of extinction (Buckland et al., 2014b), while the other 12 are in patches of high quality native forest surrounded by unsuitable invaded forests (Supplementary data Fig. A1 in Appendix A). One potential management option is to translocate geckos from some or all of the 18 threatened subpopulations of *P. guimbeaui* to better quality habitats that are not at risk of further erosion or loss (Buckland et al., 2014b). However, matching habitat suitability and availability at a potential release site to a species' needs is central to a translocation or reintroduction programme (IUCN, 2012).

We quantified habitat selection by *P. guimbeaui* with a use-availability design at three hierarchical spatial scales (Thomas and Taylor, 1990) to inform potential management decisions. First, home range sizes and pattern of temporal overlap were compared between the sexes. We hypothesised that *P. guimbeaui* would be similar to other Mauritian *Phelsuma* species in that male home ranges would be larger, overlapping with several females but avoiding other males (Gerner, 2008). Since age may also influence habitat selection (Alldredge and Griswold, 2006), population-level habitat selection was compared between age groups. Since *P. guimbeaui* is arboreal, we expected that individual tree characteristics and species diversity would influence selection. Due to size differences between the age groups, we predicted adults would be selecting habitats with higher tree diversity, more cavities, and taller trees with a higher diameter at breast height (dbh) (Harmon et al., 2007). Finally, we investigated the order of importance of each habitat predictor for *P. guimbeaui* at the three different levels, as well as differences between sexes at the home range and microhabitat level. We hypothesised that *P. guimbeaui* would show a strong selection for habitat heterogeneity, particularly high tree diversity and tall trees with a large dbh and high cavity density (Bungard, 2000; Cole, 2005; Harmon et al., 2007). We then used these data to make recommendations for the conservation of *P. guimbeaui*.

2. Study area

The study was conducted between 1 June 2010 and 20 May 2011 in the Black River mountains in southwest Mauritius (Supplementary data Fig. A1 in Appendix A). The study site was selected because it is one of the most undisturbed dry forests (Page and d'Argent, 1997) in which *P. guimbeaui* still survives. The study site was 0.5 km^2 in size and the elevation ranged between 213 and 223 m; monthly rainfall varied from 0.0 to 357.4 mm and average monthly temperature from 21.7 to 27.6 °C. Based on monthly rainfall data, the dry season was from June 2010 to December 2010 (monthly mean ± SE 12.1 ± 4.2 mm, range 0.0–31.0 mm, $n = 7$), and the rainy season from January 2011 to May 2011 (mean ± SE 182.7 ± 60.2 mm, range 22.3–357.4 mm, $n = 5$).

3. Materials and methods

3.1. Study species

P. guimbeaui is sexually dimorphic. Adult males have a snout-to-vent length (SVL) of 45–60 mm, distinctive hemipenal swellings at the base of the tail and bright colouration. Adult females are smaller, with a SVL length of 40–50 mm, no hemipenal swellings, occasional calcium sac swellings on the neck, and a pear-shaped body with moderately bright colouration. Sub-adults have a SVL length of 40–45 mm with indistinct adult colouration and no sexual characteristics, and juveniles have a SVL length of <40 mm with dull greyish colouration. The different age groups were easily differentiated in the field using these features.

P. guimbeaui is restricted to the western part of mainland Mauritius. There are 30 known subpopulations occupying small isolated fragments of habitat ranging from 0.006 to 1.0 km^2, with a combined area of 10.3 km^2 (Buckland et al., 2014b). Some subpopulations occur in sympatry with *P. ornata* (ornate day gecko) and *P. cepediana* (blue-tailed day gecko).

3.2. Vegetation survey

Nine random 16 × 16 m quadrats were set up within the study site. Pilot studies showed that trees with a dbh < 5.0 cm were rarely used by *P. guimbeaui*. Therefore, within each quadrat, we numbered all the trees with a dbh ≥ 5 cm, identified them to species, and recorded dbh to the nearest 1 cm, visually estimated tree height to the nearest 25 cm, and the number of cavities with a diameter > 0.5 cm (hereafter, cavity density). We added "native dead tree" as a category.

3.3. Data collection

Twenty-minute visual estimate surveys (VES) were conducted within each quadrat on a weekly basis for one year. These consisted of a slow-paced walk along a set route within the quadrat either in the morning (07:00–10:00) or afternoon (15:00–18:00), the main activity periods of *P. guimbeaui*. Each tree was systematically inspected and age group, sex (whenever possible), tree number and X/Y coordinates were recorded for each gecko detected. We photographed the dorsal view of each gecko and photo-recognition was used to identify individuals (Wanger et al., 2009) from their unique dorsal pattern. Only complete and focused images were used to reduce the risk of misidentification. While *Phelsuma* can change their colour and thereby mask their pattern, particularly when stressed or cold, no significant colour changes were observed during the periods of peak activity.

We used those adult geckos that were regularly detected to calculate home ranges. To detect possible movements by known geckos inside and outside each quadrat, a focal search was conducted for approximately 30 min two to five times per week in addition to the weekly VES. The focal searches covered a radius up to 10 m from the tree on which a particular gecko was last sighted. If detected, the gecko's dorsal pattern was photographed and visually matched with previous photographs to confirm identity.

3.4. Home range estimation and temporal overlap

The small distances between sightings of each gecko meant that standard hand-held GPS recordings were too inaccurate and so the distance (x in km) and bearing (θ in radians) from the central point (CP) within the quadrat were recorded for each gecko sighted. The latitude (Y) and longitude (X) of each gecko relative to the CP was calculated using the following formulae:

$$X = [\text{asin}(\sin(\text{CPlat}))(\cos(xd)) + (\cos(\text{CPlat}))(\sin(xd))(\cos\theta)]\pi/180$$
$$Y = [\text{CPlon} + \text{atan2}(\cos(xd)) - (\sin(\text{CPlat}))(\sin X)(\sin\theta)(\sin(xd))(\cos(\text{CPlat}))]\pi/180$$

where $xd = (x(360/((2\pi)(6371)))(\pi/180))$, CPlat is the latitude from the CP in radians, and CPlon is the longitude from the CP in radians.

To calculate home ranges, we used 100% minimum convex polygons (MCPs) (Börger et al., 2006; Kemink and Kesler, 2013; Kesler et al., 2010) so that we could examine habitat selection within the maximum area available to each adult gecko. MCP estimates were generated in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA) using Hawth's tool (Beyer, 2004). Individual geckos were not sighted an equal number of times, and so home ranges were estimated using a different number of sightings for each gecko. This can affect estimates of home range size (Laver and Kelly, 2008), and so we used a generalised linear model to assess the relationship between home range size (response) and the number of sightings used (predictor). If the relationship was significant ($P < 0.05$), the home range estimate with the lowest number of sightings was removed and the model rerun. This was repeated until the relationship between home range size and number of sightings was no longer significant. The same procedure was conducted for the number of days each gecko was monitored.

Temporal overlap was defined as two or more adult geckos observed simultaneously in the same tree and was calculated monthly and across the whole monitoring period.

3.5. Statistical analysis

All statistical analyses were conducted in R (R 2.15.3 Development Core Team 2013). Prior to model selection, all variables were tested for multicollinearity using a pairwise correlation test. To minimise problems due to collinearity, which can lead to convergence failures, we subtracted the mean from each raw value and then divided by the standard deviation for each variable (Logan, 2011). All possible model candidates were generated in the R package *MuMIn* (Bartoń, 2013). Generalised linear mixed models (GLMMs) were implemented in the *lme*4 R package (Bates et al., 2013). We found the best (most parsimonious) model using the corrected Akaike information criterion (AICc) because the sample size (n) divided by the number of parameters (K) was less than 40 (Burnham and Anderson, 2002). Generalised linear models (GLMs) and GLMMs using count data were checked for overdispersion by testing whether the variance was more than expected.

We used coefficient of determination (R^2) as a standardised effect size statistic to determine the amount of variation explained by a model (Nakagawa and Cuthill, 2007; Nakagawa and Schielzeth, 2013). For non-mixed effects models, we used pseudo R^2 Nagelkerke's statistic (Nagelkerke, 1991) to estimate the percentage of variance explained in the best model. We further determined the variance explained by each predictor within the best model by calculating the partial Nagelkerke's

R^2 by successively removing a predictor and estimating the difference in R^2 (Schradin et al., 2010). For mixed-effects models, we implemented the marginal R^2 (Nakagawa and Schielzeth, 2013) to explain the variance of the fixed effects predictors only. Following the same procedure as with partial Nagelkerke's R^2, we calculated the variance explained by each fixed effect predictor. All calculations were conducted in the package *MuMIn* (Bartoń, 2013).

Modelling results are reported as *P*-values, partial Nagelkerke's R^2 or marginal R^2, while mean values of predictors are given as mean ± SE unless stated otherwise. If the 95% confidence interval of the parameter estimate did not include zero, we concluded that it had an effect on the response variable (Mazerolle, 2006).

3.5.1. Home range and temporal overlap

We used a general linear model to investigate the effect of sex on home range area, using normalised home range area (log-transformed) as the response variable and sex as the predictor variable. We included the number of monitoring days and number of sightings as independent covariates to control for variation in the number of sightings and sampling effort. To examine temporal overlap between males and females, and within each sex, GLMs were constructed using a Poisson error structure with a log link function; the number of times another gecko was seen sharing the same tree was included as a response variable and sex as the predictor variable. Models were tested monthly and for the whole year.

3.5.2. Habitat selection at the population level

A Poisson GLMM with a log link function was used to analyse the effects of habitat on the abundance of each age group. The number of sightings was the response variable, with cavity density, dbh, tree height, season (dry or rainy), tree species and two-way interactions between cavity density, dbh and tree height as fixed effects. Tree number was included as a random factor to adjust for within variation and repeated use by individual geckos. Only tree species with more than 5 trees and 20 gecko sightings (Supplementary data Table A1 in Appendix A) were included. We plotted the mean number of gecko sightings per tree species to determine which tree species were selected by the different age groups.

3.5.3. Habitat selection at the home range level

Differences in resource use and availability with home ranges and the rest of the quadrat were examined using a binomial GLM with a logit link function. The binomial response variable was 1 for the habitats within the home range and 0 for habitats in the rest of the quadrat. Five predictor variables were tested: mean dbh of trees, mean height of trees, mean number of cavities per tree, mean number of trees (tree density) and mean number of tree species (tree diversity). We also included all two-way interactions between mean dbh, mean height and mean number of cavities per tree. The mean values of habitat predictors were used to standardise the measurements inside and outside home ranges because the spatial areas differed. The number of sightings and number of days monitoring were included as covariates to control for sampling variation in the estimation of home ranges.

Based on the results of the above model, differences in habitat selection by males and females were investigated by constructing separate general linear models for each of the selected habitat variables, using habitat feature as the response variable and sex as the predictor. Only adult geckos which stayed within the quadrat during the course of the study were included.

3.5.4. Habitat selection at the microhabitat level

Resource use and availability were assessed within individual home ranges. We used the same response variable, predictor variables and model structure as for the population scale model, with the exception of season, which was excluded because too few adult geckos had enough sightings for both seasons. A second random factor (gecko identity) was included to adjust for within variation and pseudo-replication due to repeated measures from the same geckos and trees. The number of sightings and number of days monitoring were included "as offsets" to control for their effects. We plotted the mean number of sightings per tree species to determine which species were selected by the adult geckos. General linear models and GLMs (Poisson family) were used to determine whether sex had an effect on habitat selection, with habitat features as the response variables and sex as the predictor. Only tree species with more than 5 trees and 20 gecko sightings (Supplementary data Table A1 in Appendix A) were included.

4. Results

We recorded 620 trees with a dbh > 5 cm in the nine quadrats; there were 21 native and four exotic species (Supplementary data Table A1 in Appendix A). Of these trees, 85.6% were native, 10.9% native dead and 3.5% exotic. Mean cavity density ± SE was 2.2 ± 0.4, range 0–111, mean dbh ± SE was 10.4 ± 0.3 cm, range 5–89 cm, and mean height ± SE was 4.25 ± 0.05 m, range 1.25–10.00 m; all $n = 620$.

We detected no significant multi-collinearity between the different predictors (correlation factor < 0.7). We found no effects of sampling effort at any level of hierarchical habitat selection. No over-dispersion was observed in the count data predictors in the GLMMs, but a quasi-Poisson distribution was implemented whenever it occurred in the GLMs.

Table 1
Population-level effects of cavity density, tree dbh, tree height, season and tree species on the number of sightings of adult, sub-adult and juvenile *P. guimbeaui* in a mixed-effects model. The figures are parameter estimates (Par. est.) with standard errors (Std. err.) and marginal R^2 (Mar. R^2); bold indicates $P < 0.05$.

	Adult			Sub-adult			Juvenile		
Fixed effects predictors	Par. est.	Std. err.	Mar. R^2	Par. est.	Std. err.	Mar. R^2	Par. est.	Std. err.	Mar. R^2
Cavity density	**0.25**	**0.11**	3.34	0.19	0.11	2.13	0.12	0.09	1.33
Tree dbh	**0.38**	**0.14**	1.23	0.28	0.15	0.33	0.14	0.13	0.71
Tree height	**0.37**	**0.13**	8.56	**0.30**	**0.15**	3.55	**0.36**	**0.13**	6.40
Season	**−1.17**	**0.06**	4.82	**−1.70**	**0.21**	10.09	**−1.56**	**0.17**	10.52
Tree species			9.66			7.88			5.50
Native dead tree	**−0.80**	**0.29**		**−1.67**	**0.33**		**−1.40**	**0.28**	
Diospyros sp.	0.44	1.09		−0.01	1.24		−0.71	1.41	
Eugenia lucida	−0.16	0.35		−0.33	0.41		−0.27	0.35	
Eugenia sieberi	0.02	0.40		−0.67	0.50		−0.44	0.40	
Fernelia buxifolia	**−1.92**	**0.60**		**−2.00**	**0.90**		−1.07	0.54	
Foetidia mauritiana	0.36	0.69		−0.03	0.77		0.57	0.60	
Haematoxylum campechianum	−0.33	0.92		−1.74	1.29		0.33	0.81	
Hilsenbergia petiolaris	0.15	0.53		0.01	0.57		0.38	0.47	
Ludia mauritiana	−0.39	0.57		−1.07	0.83		−1.47	0.83	
Ochna mauritiana	−1.74	0.83		−0.81	0.84		−1.39	0.86	
Scolopia heterophylla	**2.64**	**0.57**		**1.44**	**0.57**		**1.27**	**0.49**	

4.1. Home range attributes

A minimum of 35 sightings ($F_{1,29} = 4.1$, $P > 0.05$, $R^2 = 13.0\%$) and 84 days monitoring ($F_{1,29} = 3.4$, $P > 0.05$, $R^2 = 11.0\%$) were needed to calculate asymptotic home ranges. Of 105 adult geckos, 28 (12 males, 16 females) had enough sightings and number of days monitoring for further analyses; for these the mean number of sightings was 61.9 ± 4.1 (range 36–124) and mean number of days monitored was 241.4 ± 13.6 (range 84–346; Supplementary data Table A2 in Appendix A). Males had significantly larger home ranges than females; mean ± SE male home range size 77.0 ± 14.0 m^2, range 31.6–158.3 m^2, $n = 12$; mean ± SE female home range size 26.6 ± 5.5 m^2, range 1.9–67.6 m^2, $n = 16$; $t_{24} = 3.5$, $P < 0.005$, $R^2 = 37.3\%$.

On a monthly basis, significantly fewer adult males than females were seen within adult male home ranges; mean ± SE male sightings 0.3 ± 0.1, range 0–1, $n = 12$; female sightings 1.8 ± 0.5, range 0–6, $n = 16$; $z_{22} = -3.1$, $P < 0.001$, $R^2 = 45.6\%$. There was no significant difference in the number of adult male and female geckos seen within adult female home ranges; mean ± SE male sightings 1.2 ± 0.1, range 0–2, $n = 12$; female sightings 1.2 ± 0.2, range 0–3, $n = 16$; $z_{30} < 0.001$, $P > 0.5$, $R^2 < 0.001\%$ (Supplementary data Table A2 in Appendix A).

Patterns of temporal overlap were similar across the year, with significantly fewer other adult males than females seen within male home ranges; mean ± SE male sightings 0.6 ± 0.2, range 0–2, $n = 12$; mean ± SE female sightings 3.8 ± 0.9, range 1–13, $n = 16$; $z_{22} = -4.6$, $P < 0.001$, $R^2 = 74.3\%$. However, there was no significant difference between the number of adult males and females seen within adult female home ranges; mean ± SE male sightings 2.0 ± 0.2, range 0–4, $n = 12$; mean ± SE female sightings 1.9 ± 0.3, range 1–4, $n = 16$; $z_{30} = 0.3$, $P > 0.5$, $R^2 = 0.2\%$.

4.2. Habitat selection at the population level

The best model in each age group included cavity density, dbh, height, season and tree species as predictor variables and explained 27.6% of the variance for adults, 24.0% for sub-adults, and 24.5% for juveniles. Independent of age group, tree species, tree height and season had moderate effect sizes, with tree height and tree species having positive effects on gecko abundance (Table 1). The endemic tree *Scolopia heterophylla* was strongly selected, while the endemic *Foetidia mauritiana* and *Hilsenbergia petiolaris*, and the exotic *Haematoxylum campechianum*, were moderately selected by all three age groups (Fig. 1A–C). There were significantly fewer sightings in the rainy than the dry season (Table 1). Rainfall could be linked either to increased mortality or a lower probability of detection. The latter seems more plausible as weather conditions affect the detectability of geckos (Buckland et al., 2014a; Imlay et al., 2012). In addition, the higher effect size observed in sub-adults and juveniles in the rainy season could be related to their smaller size and duller colours, which made them harder to detect in poorer light conditions. For adults, cavity density and dbh had significant positive relationships with the number of sightings, but with smaller effect sizes, whereas there were no significant relationships for sub-adults and juveniles, which were related to the small effect sizes (Table 1).

4.3. Habitat selection at the home range level

At the home range level, the best model contained tree density and tree diversity as predictors and accounted for 61.0% of variance. High tree diversity had a large effect size on home range selection ($z_{53} = 3.0$, $P < 0.005$, $R^2 = 56.3\%$), whereas tree density had no effect ($z_{53} = -1.8$, $P > 0.05$, $R^2 = 4.7\%$). Within home ranges, males were selecting habitats with less tree diversity than females ($t_{26} = -2.3.4$, $P < 0.05$, $R^2 = 16.9\%$).

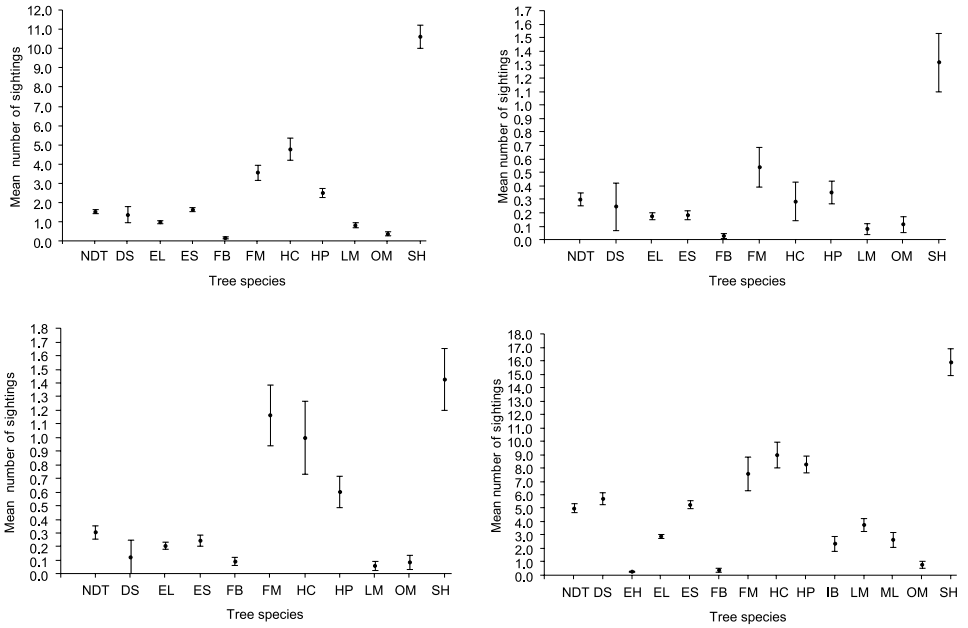

Fig. 1. The use of different plants species at different spatial scales and age groups at the population level. A—adults at the population level; B—sub-adults at the population level; C—juveniles at the population level; D—adults at the microhabitat level. NDT—native dead tree; DS—*Diospyros* sp.; EH—*Erythroxylum hypericifolium*; EL—*Eugenia lucida*; ES—*Eugenia sieberi*; FB—*Fernelia buxifolia*; FM—*Foetidia mauritiana*; HC—*Haematoxylum campechianum*; HP—*Hilsenbergia petiolaris*; IB—*Ixora borboniae*; LM—*Ludia mauritiana*; ML—*Molinaea laevis*; OM—*Ochna mauritiana*; SH—*Scolopia heterophylla*.

Table 2
Microhabitat-level effects of cavity density, tree dbh, tree height and tree species on the number of sightings of known adult *P. guimbeaui* in a mixed-effects model. The figures are parameter estimates (Par. est.) with standard errors (Std. err.) and marginal R^2 (Mar. R^2); bold indicates $P < 0.05$.

Fixed effect predictors	Par. est.	Std. err.	Mar. R^2
Cavity density	0.22	0.15	1.08
Dbh	**0.36**	**0.14**	5.09
Height	**0.29**	**0.12**	5.24
Tree species			16.41
Native dead tree	−**1.56**	**0.40**	
Diospyros sp.	0.16	0.64	
Erythroxylum hypericifolium	−**2.37**	**0.70**	
Eugenia lucida	−0.11	0.47	
Eugenia sieberi	0.17	0.50	
Fernelia buxifolia	−1.61	0.82	
Foetidia mauritiana	0.51	0.92	
Haematoxylum campechianum	0.35	0.97	
Hilsenbergia petiolaris	0.32	0.67	
Ixora borboniae	−0.93	0.98	
Ludia mauritiana	0.87	0.71	
Molinaea laevis	0.35	0.98	
Ochna mauritiana	−1.27	0.90	
Scolopia heterophylla	**2.62**	**0.70**	

4.4. Habitat selection at the microhabitat level

At the microhabitat level, the best model contained cavity density, dbh, tree height and tree species as predictor variables and accounted for 27.8% of the variance in the number of sightings. The results were similar to those at the population level, except that cavity density had a small effect size and no significant effect on the number of sightings (Table 2). Tree species selection was similar to adult geckos at the population level (Fig. 1A, D). Habitat selection was not significantly different between males and females: cavity density ($t_{409} = 0.2, P > 0.5, R^2 < 0.001\%$), dbh ($t_{409} = 0.7, P > 0.5, R^2 = 0.1\%$) and tree height ($t_{409} = -0.04, P > 0.5, R^2 < 0.001\%$).

5. Discussion

We tested three hypotheses on habitat selection by *P. guimbeaui* in one of the least disturbed areas of surviving lowland dry forest in Mauritius rather than a disturbed habitat since we considered this would be a better indicator of the habitat requirements of *P. guimbeaui*. Quantifying the spatial and habitat requirements of *P. guimbeaui* in a native habitat is more informative when searching for potential translocation sites. By including a wide range of habitat predictors, we have provided a thorough understanding of habitat selection by *P. guimbeaui* at different spatial scales. For adult geckos, a positive effect was recorded for tree diversity at the home range level; cavity density, dbh and tree height at the population level; and tree height and dbh at the microhabitat level. At the population level, different age groups were choosing different habitat features: adults selected taller trees with larger dbh and higher cavity density, whereas sub-adults and juveniles only selected taller trees but not dbh or cavity density. Irrespective of age group, *S. heterophylla* was strongly selected, *F. mauritiana*, *H. campechianum* and *H. petiolaris* were moderately selected.

5.1. Spatial and habitat requirements

As predicted, male *P. guimbeaui* had larger home ranges than females and overlapped with females more often than with other males. A larger home range overlapping with several females potentially enhances a male's reproductive success (Haenel et al., 2003; Perry and Garland, 2002; Rose, 1982; Schoener and Schoener, 1982). Size and location of female home ranges are related to key resources such as food and shelter (Stamps, 1983). Why female home ranges overlapped is less clear: this could reflect resource availability.

While tree species or tree diversity were the most important habitat features selected by *P. guimbeaui* at all three hierarchical levels, the effect size of tree diversity ($R^2 = 56.3\%$) was largest at the home range level. There are two possible explanations. *P. guimbeaui* is mainly insectivorous. Habitats with a higher plant diversity have greater insect diversity (Florens et al., 2010; Herrera and Dudley, 2003; Marini et al., 2010) and hence an increased abundance and diversity of prey items. This could explain why female *P. guimbeaui* selected habitats with a higher tree diversity. An increase in tree diversity could also be linked to a more complex branching structure (Bungard, 2000; Cole, 2005), increasing the number of perches available for thermoregulation (Harmon et al., 2007).

Tree height was the second most important predictor of gecko sightings across age groups and spatial scales. This is also important for thermoregulation: taller trees provide a greater heterogeneity of basking sites through the day and hence increase the ability of the geckos to thermoregulate. Thermoregulation is essential for foraging, digestion and flight responses (Smith and Ballinger, 2001).

At the population level, cavity density and dbh had a significant effect on adult sightings, albeit with small effect sizes. Cavities are important for adult *P. guimbeaui* because they provide protection from avian predators (being at greater risk of predation, gravid females were invariably seen close to a cavity), cover for their "sit and wait" foraging, safe egg-laying sites, good thermoregulation sites and shelter when inactive or during poor weather conditions (Bungard, 2000; Cole, 2005). Trees with a greater dbh provide a greater range of thermoregulatory sites. However, cavity density and dbh did not have an effect on the number of sub-adults and juveniles, probably because the adults excluded them from optimal habitats (Rummel and Roughgarden, 1985; Schoener et al., 2001).

5.2. Implications for conservation

Although *P. guimbeaui* has not yet been classified by the IUCN, it is the most threatened endemic species of *Phelsuma* surviving in Mauritius, and many of the 30 known subpopulations are currently under imminent risk of extirpation. However, *P. guimbeaui* plays important ecological roles at several trophic levels, contributing to ecosystem function and stability, thereby helping to reduce the loss of biodiversity (O'Gorman and Emmerson, 2009). One management option is to translocate the 18 most threatened subpopulations (i.e. those in patches of exotic forest) to one or more secure locations (Buckland et al., 2014b), or move them to reinforce the more secure subpopulations that survive in patches of endemic forest (Seddon, 2010). Despite being widely used as a conservation tool, translocation success has been relatively low, possibly due to a failure to determine habitat quality at release sites (Stamps and Swaisgood, 2007). Selecting release sites with good quality habitat is key to successful translocation programs (Griffith et al., 1989), particularly for species such as *P. guimbeaui* where effective population sizes are already low (Buckland et al., 2014b).

Translocation usually involves the movement of threatened species within or outside their historical range (IUCN, 2012). However, habitat fragmentation and lack of connectivity between the remaining small fragments of high quality native forest in Mauritius (Buckland et al., 2014b) means that conservation reinforcement and re-introduction (see definitions in IUCN, 2012) would be inappropriate for *P. guimbeaui*. Because the 18 most threatened subpopulations are in small isolated patches of four types of exotic forest (Buckland et al., 2014b), the only practical option for these subpopulations is conservation introduction (assisted colonisation) to new sites outside *P. guimbeaui*'s known historical range. These 18 subpopulations have been isolated for approximately 0 to 239 years (Buckland et al., 2014b) and so could be locally adapted to their respective environments. However, these exotic forests and our study site shared similar tree characteristics i.e. large numbers of cavities, large dbh and/or tall trees. This suggests that *P. guimbeaui* could be locally adapted to similar

environmental conditions and so moving geckos between habitats would not be an issue. Furthermore, finding lowland native woodland with the right habitat features is likely to prove problematic on mainland Mauritius, and releases on offshore islands already designated for conservation may be a more practical option. It would also minimise the risks posed by invasive species on mainland Mauritius, particularly *P. grandis* (Buckland et al., 2014a).

In addition to identifying key habitat features at potential translocation sites, our data also highlight the importance of increasing tree diversity within existing sites. The 12 least threatened subpopulations (Supplementary data Fig. A1 in Appendix A) are in patches of native woodland surrounded by highly degraded forests containing dense growth of exotic trees such as *Psidium cattleianum* (strawberry guava). Tree diversity within invaded forests is usually low (Baider and Florens, 2011), and *P. cattleianum* has limited branching and no cavities, so lacks the structural complexity required by *P. guimbeaui*. The dense growth of *P. cattleianum* also prevents sunlight penetrating the understorey and so is likely to limit the ability of *P. guimbeaui* to thermoregulate. Habitat restoration through weeding and planting native species enhances faunal abundance (Florens et al., 2010), particularly endemic *Phelsuma* (Cole, 2005). Restoring the highly invaded forests surrounding these 12 subpopulations of *P. guimbeaui* will be key to their long-term conservation. While our findings highlight the importance of conducting habitat suitability research prior to conservation intervention and habitat restoration, data are also required on other population processes to enhance translocation success (IUCN, 2012; Moseby et al., 2011; White et al., 2012).

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.06.001.

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